ORDERS OF INSECTS WITH HEART-BEAT REVERSAL

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Introduction

Intermittent (periodic) reversal of direction of heart-beat, formerly regarded as limited to the Ascidea, has been described by Bethe (1927) as normally occurring in *Phoronis psammophora*.

A similar but transitory intermittent reversal in the embryo before normal direction is established has been observed by Bremer (1931–32) in the chick and by Yokoyama (1929) in the silkworm. In the former it appears to be of rare occurrence; in the latter a characteristic of the embryo anticipating the normal periodic reversal to be seen in the prepupa, pupa, and imago.

In response to experimental conditions, reversal of heart-beat during early development of a teleost (*Macropodus viridi-auratus*) was noted by Gowanloch (1923) and in the chick embryo by Johnstone (1925).

Since the publication of my paper (Gerould, 1929)[1] describing the wide-spread and probably universal occurrence of this phenomenon in Lepidoptera after the larval stage with its forward beating has passed, I have observed it in other orders of holometabolous insects. In none of the orders with complete metamorphosis, except possibly Neuroptera (*Corydalis*) not yet thoroughly examined, have I failed to find examples of it in the imago.

Diptera

In a crane fly, *Pachyrhina ferruginea*, peristalsis of the dorsal vessel was observed with extraordinary clearness through the translucent integument of the abdomen. Previous experience with moths had shown that removal of head and appendages does not prevent or seriously affect periodic reversal. The head, wings, and legs were accordingly removed, and peristalsis was observed in abdominal segments 3–5.

I have rarely seen in any insect such a regular series of short alternating phases. In this respect this crane fly resembled the adult

[1] Attention should be called to an error in this paper on p. 426, line 8, referring to pulse rate; "forward" should read "backward." The sentence should read: "It (average pulse rate in forward beating) is roughly twice as fast as in backward beating."

Bombyx mori rather than the pupa or prepupa of that moth. As shown by Table I taken from my first observation (August 16, 1930; temperature 24° C.), the forward phases averaged about 60 beats, the backward about 36; numbers remarkably similar to averages obtained with young silk-moths, which were 51.7 beats forward, 26.5 backward.

The rate of forward beating in the moth was 10 beats in 17 seconds, backward 10 in 29 seconds, but in the crane fly these data show a nearly equal rate in each direction (average 9.9 seconds forward, 9.5 seconds backward). (See Table II). Of especial interest was the regularity with which the rate of backward beating was accelerated during each backward phase, in contrast to the gradual retardation that took place

TABLE I

Heart-beats of the crane fly, Pachyrhina ferruginea (male)

No. Beats in a Phase		No. Beats in a Phase	
Forward Phase	Backward Phase	Forward Phase	Backward Phase
30 + 14 = 44	39	63	35
60 + 16 = 76	38	57	38
53 + 16 = 69	38	63	
64	37	56 + 6 = 62	36
59	34	51 + 5 = 56	36
51		65	34
Av.	60.5 37.2	Av.	60.1 35.8

during the forward phases. Such acceleration was observed in *Bombyx* only during the long backward phase immediately preceding and during pupation.

The regularity in the number of beats in the forward phases in this crane fly was soon interrupted by spontaneous activity of the genitalia, which partially inhibited forward beating and reduced the length of the forward phases from an average of 60 beats to about 30, while the alternate backward phases remained of about the same length as previously.

The same preparation 18 hours later (kept in a moist chamber overnight) showed persistent backward beating, broken at first by pauses into groups of about 36 beats. Over 500 beats were counted, and 37

groups of 10 beats were recorded which showed practically no change in rate (10 beats in 10 seconds).

Observations on a drone fly, *Eristalis*, in which beating is extremely rapid, gave among others the following result. Gradual retardation of pulse rate during backward beating is evident. (See Table III).

Coleoptera

In the Coleoptera, no published statement in regard to periodic reversal has come to my attention, though Lasch (1913) in studying the

Table II

Heart-beats of the crane fly (male), Pachyrhina ferruginea. Temperature 22.5° C.

No. Seconds Required for 10 Beats		No. Seconds Required for 10 Beats	
Forward Phase	Backward Phase	Forward Phase	Backward Phase
7, 9, 10	10.5, 8	7, 9, 9.5	12, 8.5
7, 9, 9.5, 10	11, 7	8, 10, 11.5, 10.5	12
7.5, 9.5, 10.5	9.5, 9	9.5, 9	9.5, 8
8, 8.5, 10.5	9		11, 7
	12, 9		

Retardation — Acceleration

larva of the stag-beetle, *Lucanus cervus*, observed in a few normal larvae a single backward wave extending through a few segments, and in one individual injured by artificial stimulation he saw a succession of backward waves extending through several segments, or merely from one into the next one behind it. His observations, however, were apparently limited to the larva, in which normal periodic reversal is not to be expected.

In August 1931 and again in 1932 I made observations on a large beetle, *Prionus laticollis*. The first individual studied was a ♀ found moribund with leg reflexes still feeble; but, as is generally the case in insects, heart action continued long after leg reflexes had ceased.

It was first observed (4:30 P.M.) by slitting each side of the back and pinning back the body wall so that the ventral surface of the dorsal vessel could be seen; there was vigorous double-action or central beating from the front part of the metathorax, forward through the aorta to the head and backward in the abdominal vessel, in which the rates counted successively were 10 beats in 17, 19, 19, 18, 19, 21, 21, 24 seconds. At 5 P.M. there was again central beating. Counts of the forwardly directed waves in the thorax gave 10 beats in 15, 15, 15 seconds, and during the same phase but backward through the abdomen 10 in 18 seconds (temperature 29° C.).

Kept 18 hours in a moist chamber, the head end of the aorta had

TABLE III

Heart-beats of the drone fly, Eristalis, with abdomen laid open.
Temperature 25° C.

No. Seconds for 10 Beats	No. Seconds for 10 Beats
Forward Phase	Backward Phase
3.5, 3.5, 3, 2.5, 2, 3 →	→ 4, 4.8, 4.5, 5.5, 5, 5, 6, 5, 5.5, 5, 6, 6.5, 5.8, 6, 6.5, 10, 12.5, 9.5
→ 4, 4, 5.5, 5	

become dry at 10:50 A.M., but backward peristalsis from the anterior part of the metathorax through the abdomen was proceeding at the rate of 10 beats in 21.5, 22 seconds; for a few minutes double or triple beats went backward from the metathorax, but at 11:13 A.M. the groups of two or three had been reduced to single beats with the rate of 10 in 15, 16, 16 seconds. (Temperature 25.5° C.).

In August of the following year, a much longer series of observations was made on a ♂ *Prionus laticollis* which was etherized slightly before the removal of mandibles, antennae, legs, and wings (2:33 P.M., August 6; temperature 29° C.). It was first viewed through the translucent anterior segments of the abdomen. Forward beating at the rate of 10 beats in 9.8, 10.8 seconds was followed by backward, 10 beats in 9, 9 seconds. Then a forward phase was followed by a backward phase of over 300 beats beginning at a rate of 10 beats in 6, 7.25, 7.25 seconds.

The backward beating was slightly more rapid than the forward. After amputation of the head, a series of forward waves began at the rate of 10 beats in 8.6 seconds and ended with 10 in 9.5 and 10 seconds. Air sucked into the dorsal vessel interfered with observations, so a preparation was made of the excised back, showing the ventral surface of the abdominal dorsal vessel, the front of which was inflated with air. Thereupon backward beating started in the inflated anterior part and the following records of the duration of 10 beats were taken: 10 in 9.5, 10, 9, 10.5, 9.5, 10.5, 11, 10.5, 11, 11, 11, 12.25, 12, 12.5, 12, 12.4, 13, 13.5, 14, 15, 14, 14.6, 15.6, 16.5, 16.5, 17, 19 seconds. Beating both ways from the middle of the abdomen followed, freeing the front of the tube of the contained air, the rate of beating steadily falling: 10 in 19, 19.5, 20, 20, 21, 21, 23.5 seconds. The preparation, now drying, was moistened with normal saline solution, and completely forward beating began at a more rapid rate, viz., 10 in 5.5, 7, 8, 9, 9, 8.6, 9.5, 9.5, 9.6, 9 seconds. Then completely backward beating through the whole abdomen ensued; 10 beats in 9.5, 9.5, 9.6, 9.5, 9.5, 9.5, 9.5, 9.6, 9.5, 10, 10, 10, 10.5, 9.6, 10.6, 11, 11.4, 11, 11, 11.25, 11.2, 11, 11, 11, 11, 11.5, 11.5, 11.5, 11.5, 11.5, 12, 12, 12.5, 11.8, 12.5, 12.2, 11.8, 12.2, 12.5, 11.5, 12.2, 11.8 seconds. Then central beating; 10 in 12 (double strokes), 11.5, 11.5, 11, 11, 12 seconds (pausing after the seventh). Then forward altogether: 10 in 12, 12, 11, 12, 11, 11, 11.2, 11.2, 10.5, 11.8, 12, 12, 12, 11.8, 11.2, 11.5, 11.4, 11.2, 11.2, 11.2, 11.6, 12, 12, 11.5, 11.8, 12, 12.75, 11.5, 12.5, (moistened) 11, 11, 13, 12, 12.5, 12, 12.75, 12.2, 12.6, 13, 12.6, 14.6, 16.2, 16.6, 17 seconds. On flooding with saline solution, forward beating continued at increased rate: 10 beats in 7.5, 6.5, 6.5, 7.5, 6.5, 7.2, 7, 7, 8, 8, 8.8, 8.2, 9, 9.5, 9.5, 10, 11, 12, 11.5 + (pause after 7). Reverses, a few beats backward, then forward; pause of 10 seconds, then backward; pause of 17 seconds, then forward, then backward. Length of the observations 2.5 hours (2:33–5:03 P.M.), temperature at the end 29° C. as at the beginning.

The following morning the preparation was alive (in moist air) and a long phase of forward beating observed, the rate of which showed gradual and regular retardation. At first there were pauses between each group of about 10 beats. A succession of counts showed 10 beats (forward) in 5.8, 5.8, 6.5, 6.2, 7.4, 6.6, 6.5, 7.5, 6.8, 6.8, 7, 7.5, 7.5, 7.6, 7.6, 8, 8.5, 7.5, 8, 8, 8, 8.2, 8, 9, 10, 10.5, 11, 10, 10, 10 seconds. There were now less than 10 beats in a phase, and soon groups of 2 beats came; counts of 10 pairs (forward) in 17.5, 19.5, 18, 19, 20, 20, 20, 20, 21, 20.6, 21, 22 seconds. Now single beats replaced pairs and counts of 10 gave 24, 25.4, 24.5, 28, 28, 25.5, 25, 27, 29, 28, 29, 26.5, 29, 33 seconds and beating stopped. Saline solution was applied, and a

series of converging beats conflicting at the third abdominal segment (backward in front of the third segment but still forward behind it) gave the following series of counts: 10 beats in 9.5, 8, 7.5, 8, 7, 8, 7.5, 7.5 seconds.

The same preparation 24 hours after the first observations, temperature 28.5° C., showed a long run of short groups of backward beats separated by pauses of about 10 seconds. There were groups of 7, then of 5 in 3, 4, 4, 3.8, 3.2, 3, 2.5 seconds.

TABLE IV

Heart-beats of solitary wasp, *Sphex*, without head or wings, first three abdominal segments observed. Temperature 28° C. First phase, observed in forward beating, lasted 25 minutes.

Forward Phase	Backward Phase
Rate 10 beats in 2 seconds	10 beats in: 2.6, 2.5, 2, 2.5, 2.5, 2, 2.5, 2.2, 2.6, 2.5, 3, 4, 3, 3.5, 2.6, 2.6, (lags), 5, 4.5, 5, 8, 9 (in flashes of 2), 14, 15, 17, 16, 26, 27.8, 32, 44.5, 83, 82 seconds, length of the phase 32 minutes, last half in groups of 2 with longer and longer pauses between successive pairs.
10 in 11 seconds	
11 seconds	
11 seconds	

HYMENOPTERA

Observations on individuals of this order are less easy and satisfactory than in other groups of higher insects for two reasons, the great length of the phases and rapidity of pulsation. Ants and bees, with their short dorsal vessels with extremely rapid beating, are particularly unfavorable. I have not yet been able to get reliable data on reversal in either group.

In a large solitary wasp, *Sphex*, however, with translucent tergum at the base of the abdomen, satisfactory proof of reversal was obtained, as Table IV shows.

This shows a backward phase of 32 minutes of exceedingly rapid beating, gradually diminishing in rate until at the end of the phase it became very slow.

An ichneumon fly, *Opheltes glaucopterus*, found moribund, reaction of appendages having ceased, gave some excellent data showing unmistakable periodic reversal, with the rapid beating and long phases

characteristic of this order. The heart was observed through the translucent tergites; body walls, head, and appendages were intact. The first observation was of a long forward phase of 27 minutes (11:23 A.M.–12 M., temperature 26.5° C.). Due to the rapid rate, groups of 20, rather than 10 beats were measured; 20 in 15 seconds at first, in 10 seconds at the end (12 readings). A second observation began at 3:20 P.M. with a backward phase of 47 minutes during which the duration of groups of 20 beats remained nearly constant, with very slight acceleration (average of 20 beats in 22.2 seconds for the first 5; 18.9 seconds for the last 5 measurements). At 5–5:08 P.M. measurements of the rate of another clearly backward phase gave an average of 18.5 seconds for 20 beats with no change. (Temperature 26.5° C.).

Orders Probably without Heart-beat Reversal

Examples of adult Neuroptera and Odonata have shown no reversal. A female dobson fly, *Corydalis cornuta*, the large size and comparatively slow pulse of which make it favorable for study, was under observation for 40 minutes; no reversal occurred. One of the Chrysopidae translucent enough for external examination showed no heart-beat reversal.

In a dragon fly, *Plathemis trimaculata*, pulsation of the dorsal vessel, observed in three males and one female, was only forward.

Summary

Representatives of four orders of holometabolous insects, Diptera, Coleoptera, Lepidoptera, and Hymenoptera have shown periodic (intermittent) heart-beat reversal in the pupa and imago. In an adult crane fly, the number of forward beats per phase exceeded the backward, but the average rates of beating in each direction were almost equal. Gradual retardation of rate occurred within each single forward phase, slight acceleration within each backward phase. In the adult beetle there was likewise no marked difference between the average rates backward and forward. A very gradual retardation in rate was observed during each phase whether backward or forward. Central beating in both directions from the pulsating vessel of the metathorax or from the middle of the abdomen occurred. A few converging waves conflicting at the third abdominal segment were observed. Saline solution quickened the rate. There was an occasional tendency to beat in groups of two without change of rate. Pauses sometimes broke up a long phase, each being of about the same length as the groups among which they were interpolated. In Hymenoptera, long backward and forward

phases, each a half hour or more in length, were characteristic of *Sphex* and *Opheltes*. The rates were rapid. In *Sphex* the rate backward was gradually retarded; in *Opheltes* the rate during any long phase was nearly constant, though during one backward phase of 47 minutes there was slight acceleration.

In general, normal reversal occurs independently of the central nervous system and is essentially myogenic. Stimuli from the head, wings, legs, and genitalia, however, secondarily affect peristalsis in detail, producing variations in rate, length of phase, number of beats in a phase, and occasionally probably reversal. Central beating does not depend upon special ganglia but upon local regions of higher irritability (or greater local inflow of haemolymph from the pericardium), which vary somewhat even in the same individual.

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